Chapter 15

Gorillas in Our Midst? Human Sexual Dimorphism and Contest Competition in Men

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INTRODUCTION

Around 500 BCE, the Carthaginian explorer Hanno the Navigator sailed south with a fleet of 60 ships along the northwest coast of Africa, encountering an island people he reported were comprised mostly of women. The men managed to escape, but Hanno's expedition captured three women who fought back so violently that they were executed by their abductors, their skins carried back to Carthage. Apparently oblivious to the hypocrisy, Hanno referred to these people as savages. His interpreters called them *Gorillai*, "tribe of hairy women" (Hanno, 1832). Over two millennia later, in 1847, Americans Thomas Savage and Jeffries Wyman borrowed this term when first describing the western gorilla (Conniff, 2009). Savage, Wyman, and the actions of Hanno's expedition were products of their times and easily strike the 21st century reader as racist and vile. We will revisit the human tendencies to classify others as in-group versus out-group, potentially regard out-group members as subhuman, and aggress against them, in our discussion of coalitional aggression in a later section.

Returning for the moment to gorillas, we note that research on these intelligent, elusive apes has revealed a wealth of information about their ecology and behavior. One of the most conspicuous aspects of gorilla social structure is that males aggressively defend groups of females from other males using their massive size, long canine teeth, and threat displays (Fossey, 1983; Maple and Hoff, 1982). Such traits are central to the behavioral repertoire of male gorillas, who experience what Charles Darwin termed *sexual selection*, a type of natural selection engendered by competition over mates (Andersson, 1994).

Since the publication of Darwin's *The Descent of Man* in 1871, a vast literature has accumulated demonstrating the salience of sexual selection in shaping the phenotypes of sexually reproducing organisms, including gorillas and humans. Sometimes referred to as "Darwin's other idea," sexual selection favors traits helpful in winning mating opportunities and is effectuated to varying degrees across species by a handful of mechanisms (Andersson, 1994). These mechanisms include *mate choice*, which favors traits desired by the opposite sex; *sexual coercion*, the use of force or threat against mates; *sperm competition*, the post-copulatory struggle for fertilization of ova that favors traits such as increased sperm production and motility; and *contest competition*, favoring traits that help win mates through same-sex physical contests and/or threatening displays directed at rivals.

Much research has focused on mate choice, though recent years have seen a reevaluation of sexual selection in humans with an increase in attention to contest competition, whose influence now seems to have been underestimated (eg, Carrier and Morgan, 2015; Hill et al., 2013; Puts, 2010, 2016; Puts et al., 2015; Scott et al., 2012). In this chapter, we consider data bearing on the influence of contest competition on men's phenotypes, but first we evaluate evidence for the overall intensity of sexual selection among ancestral men.

STRENGTH OF SEXUAL SELECTION IN MEN

A fundamental reality of reproduction in many sexually reproducing species is an asymmetry in parental

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investment: one sex, usually females, invests more in producing and caring for offspring (Trivers, 1972). Women, for example, require approximately nine months for gestation, followed by a long period of lactation and childrearing, while a contrastingly small parental effort is required for men to reproduce (Eibl-Eibesfeldt, 1989; Geary, 2000). As a result, men have a higher potential reproductive rate (Clutton-Brock and Vincent, 1991), and in natural fertility populations, there are at all times more men available to mate than there are reproductively viable women (Trivers, 1972). This skews the operational sex ratio (OSR), the number of sexually active males per fecund female, in a way that tends across species to force males into competition for the relatively few available females (Clutton-Brock and Vincent, 1991; Emlen and Oring, 1977).

The *physiological* OSR, which includes all individuals capable of reproducing, can be distinguished from the *behavioral* OSR, which includes only those engaged in mating (Marlowe and Berbesque, 2012). This may be an important distinction because the amount of time individuals are typically eligible as mating partners may exert a greater effect on sexual selection than does the amount of time individuals are physiologically capable of reproducing (Kokko and Jennions, 2008; Kokko et al., 2012). The human behavioral OSR has been estimated to be 8.6, and the physiological OSR has been estimated to be 11.7 (Marlowe and Berbesque, 2012). Regardless of which measure is used, however, the human OSR falls below orangutans (OSR = 55.0) and gorillas (OSR = 83.8), which display the highest degrees of sexual dimorphism in the primate order, and above promiscuously mating chimpanzees (OSR = 4.5), which also exhibit substantial individual and coalitional contest competition, as well as a high degree of sperm competition (Mitani et al., 1996). Hence the human OSR indicates the opportunity for moderately strong sexual selection in men.

The intensity of sexual selection is also influenced by the spatial distribution of males and females, which affects whether mates can be monopolized. Across species, female reproduction is typically limited by access to food, whereas male reproduction is limited by access to mates. Hence, females generally distribute themselves according to resource availability, as well as predation risk, and males then distribute themselves according to the distribution of females (Lindenfors et al., 2004). If females are social or otherwise spatially clustered, then one or a few males may be capable of monopolizing multiple females, and competition to be one of the few breeding males will tend to be intense (Emlen and Oring, 1977). However, if female group sizes are large, then it may be infeasible for a smaller number of males to defend them from other males, and larger multimale/multifemale groups will emerge. Male mating competition is often intense in such species, frequently taking the form of male dominance hierarchies in which dominant males gain more mating opportunities, especially with estrous females. However, in primates, canine size dimorphism and body size dimorphism tend to be less extreme in multimale/multifemale species than in species with single-male polygyny (Clutton-Brock and Harvey, 1984), probably in part reflecting less intense sexual selection.

Although humans form large multimale/multifemale groups, the human mating system is not typical of such primates, as concealed ovulation prohibits males from attempting to monopolize estrous females (Gangestad and Thornhill, 2008; Puts et al., 2013). Perhaps as a consequence, within these larger groups are embedded smaller groups of individual males mated in relatively stable and exclusive relationships to one or more females. These mateships exhibit moderate polygyny. For example, on average, 21% of married women are married polygynously across forager societies, although the degree of polygyny varies substantially across cultures and ecological contexts (Marlowe and Berbesque, 2012). As in hamadryas baboons (Schreier and Swedell, 2009), males' proprietariness over their mates helps maintain these embedded "harems" (Daly and Wilson, 1988).

Males' ability to monopolize females may also be contingent on the dimensionality of the mating environment (Puts, 2010). Males may more effectively monopolize females in environments that are one-dimensional (eg, burrows or tunnels) or two-dimensional (eg, land or floors of bodies of water), as opposed to three-dimensional environments, such as air, open water, or trees, where the region that must be defended is larger, and there are many in-routes for sexually interloping males. As a result, compared to three-dimensional mating environments, terrestrial environments may favor greater physical competition for mates, as in terrestrially breeding seals (Stirling, 1975) and turtles (Berry and Shine, 1980) relative to aquatically breeding species. Hominins have evolved in a two-dimensional environment at least since the emergence of habitual bipedalism in *Australopithecus anamensis* roughly four million years ago (Harcourt-Smith, 2007). This shift in the human paleoenvironment likely played an influential role in shaping mating behavior in our lineage. In particular, the new terrestrial environment may have enabled ancestral males to restrict sexual access to mates to a degree that was infeasible in their more arboreal ancestors.

Male mating competition also tends to increase with reproductive variance among males compared to females (Bateman, 1948). In humans, male reproductive variance exceeds that of females but this difference is highly variable across populations (Brown et al., 2009). For example, reproductive maxima have been reported as 8 and 14 for women and 23 and 43 for men among two populations of lowland South American Indians (Chagnon, 1992; Salzano et al., 1967), an approximately three-fold increase among males. However, the concentrations of wealth and power afforded by state-level societies have produced staggering reproductive variances. According to the Guinness Book of World Records, the largest number of children known to have been produced by a single woman is 69, while that for a man exceeds 1000 (Glenday, 2013). Men who are able to compete successfully for mates have the potential to produce a large number of offspring, whereas others may not reproduce at all. Women, by contrast, accrue less additional reproductive success from acquiring multiple mates—at most, they can reproduce approximately once per year, but interbirth intervals span several years in traditional societies (Blurton Jones, 1987).

It is thus unsurprising that societies allowing polygynous marriage are far more common in the ethnographic record than are those with only monogamous marriages (Murdock, 1967). Yet, even in societies with exclusively monogamous marriage, the mating system may nevertheless tend toward polygyny; men remarry (Buckle et al., 1996) and reproduce (Jokela et al., 2010) after divorce at higher rates than women (though see Borgerhoff Mulder, 2009), with reproductive variances comparable to those seen in societies with polygynous marriage (Brown et al., 2009). This pattern is not restricted to the West, the industrialized world, or the Global North—men exhibit greater reproductive variance than do women among some serially monogamous hunter-gatherers, as well (Hill and Hurtado, 1996).

The previously mentioned evidence suggests a robust potential for sexual selection in shaping men's anatomy and reproductive behavior. Women provide greater levels of parental investment through producing and rearing offspring, removing themselves from the mating pool for longer periods of time with each reproductive event. The consequent imbalance in the OSR predicts increased competition among males for mating opportunities. Men's potential to monopolize mates is reduced by women's aggregation into large groups but promoted by their terrestriality, which enables some men to defend multiple mates. As a result, men display greater reproductive variance than do women. These lines of evidence are consistent with a strong *potential* for sexual selection to shape men's phenotypes. However, sexual selection also requires nonrandom mating among men, such that men's phenotypes affect their mating opportunities. As we will now discuss, ancestral men appear to have won mates by developing traits that contributed to success in contest competition.

SELECTION FOR MALE CONTESTS

When evaluating the influence of past sexual selection on a trait, it is useful to consider several types of evidence (Table 15.1). First, high levels of sexual dimorphism suggest past sexual selection (Andersson, 1994; Darwin, 1871; Lande, 1980). Second, traits that function in mating competition are often costly to produce and maintain, and so often develop or increase in their expression at sexual maturity when they can begin to compensate for these costs. Third, if a trait affects success in one or more mechanisms of sexual selection (eg, by attracting mates or winning fights with same-sex competitors), then this suggests that the trait did so over its evolution. This may be demonstrated experimentally (eg, Andersson, 1982), or by providing correlational evidence that the trait influences success under a mechanism of sexual selection (eg, Schwagmeyer and Woontner, 1986). Fourth, if a trait affects mating success, then this indicates that it did so over its evolution. Again, experimental manipulations provide stronger evidence of causation (eg, Andersson, 1982), but correlational data can also provide evidence of a trait's influence on mating success and may have the advantage of increased ecological validity.

TABLE 15.1 Evidence of Past Sexual Selection on a Trait

- Sexually dimorphic
- Develops or increases in expression at sexual maturity
- Affects success in one or more mechanisms of sexual selection
- Affects mating success

None of these lines of evidence is sufficient by itself. For example, different ecological selection pressures such as niche partitioning can produce sexual dimorphisms, although this appears to be relatively rare (Andersson, 1994), and sexual selection may sometimes act similarly in the two sexes producing low sexual dimorphism (Hooper and Miller, 2008). In addition, if relevant aspects of the environment have changed, then a trait may currently influence mating success differently than it did ancestrally. However, in combination, these lines can provide strong evidence for past sexual selection. If a trait develops at sexual maturity, is sexually dimorphic, and appears to influence mating success through one or more mechanisms of sexual selection, then it is likely that the trait was shaped by sexual selection through these mechanisms.

Research exploring the influence of sexual selection on men's traits often emphasizes the role of female mate choice, but this emphasis may be based partly on misperceptions regarding the freedom with which women chose mates ancestrally (see, eg, Puts, 2010). Given the latitude with which women seem to choose mates in contemporary Western societies, it may surprise some readers that ancestral women probably experienced far less autonomy. For example, more than two-thirds of extant hunter-gatherer groups in a large sample had parentally arranged marriages (Apostolou, 2007), and while women may sometimes circumvent kin limitations on partner choice (eg, via "mock bride theft"; Ayres, 1974), phylogenetic analyses suggest that family members influenced mating among the earliest members of our species (Walker et al., 2011). Moreover, constraints on female choice are imposed not only by kin but also by unrelated men via sexual coercion (Puts, 2016; Puts et al., 2015a), and especially by men's exclusion of male rivals by force or threat (eg, Hill et al., 2013).

Indeed, the weight of evidence suggests that many aspects of the human male phenotype are best explained by an evolutionary history of contest competition. Contests tend to produce several types of traits that aid in excluding same-sex competitors by force or threat, including behaviors such as same-sex aggression and threat displays, and anatomical traits such as large body size and anatomical weapons (Table 15.2). If any of these traits is present, then it is a good candidate to examine for evidence of having been shaped by sexual selection via contests. As we will see, men tend to exhibit all of the hallmarks of a species that has experienced an evolutionary history of male contest competition.

Same-Sex Aggression

Across cultures, men and boys are more physically aggressive than are girls and women (Archer, 2004; Ellis et al., 2008), and men's aggression peaks at the age of greatest mating competition (Archer, 2009). Murder in particular is overwhelmingly a male phenomenon. Men greatly outnumber women in both killing and being killed everywhere that homicide has been studied (Daly and Wilson, 1988), including both subsistence societies (Beckerman et al., 2009; Chagnon, 1988; Walker and Bailey, 2013) as well as industrialized Western nations (Daly and Wilson, 1990). For example, in the Yanomamo, horticulturalists living in parts of Brazil and Venezuela, Chagnon (1988) estimated violence to account for nearly one-third of male deaths, while Walker and Bailey (2013) found the mean percentage of violent deaths among 11 traditional lowland South American societies to be 30%. Males, moreover, accounted for 69% of all such deaths, with comparable figures seen across the societies in the sample. From a wide array of human populations, Daly and Wilson (1988) report 95% of same-sex killings to be perpetrated by men, even when war-related homicides are excluded from analysis. This sex difference holds across populations even as the number of homicides changes dramatically from one to another (Daly and Wilson, 1990). As Wright (1995, p. 72) has noted, "From an evolutionary point of view, the leading cause of violence is maleness."

TABLE 15.2 Traits Favored by Contest Competition

- Physical aggression
- Large body size
- Strength
- Weapons
- Behavioral displays of formidability
- Anatomical threat displays

Of course, a male bias in physical aggression and violence, especially a bias in male-on-male aggression and violence, is predicted from the hypothesis that ancestral men competed for mates via contest competition. Physical aggression may have helped men obtain or defend mates directly, for example, by killing or injuring a competitor attempting to win the same mate (Marlowe, 2004), or attempting to steal one's mate (Chagnon, 1992), but these may have more frequently been accomplished indirectly through the threat of physical harm (see later in this chapter).

Another possible set of behavioral adaptations that may allow males to remain physically aggressive during contests relates to pain thresholds and tolerance. Physical pain signals actual or potential tissue damage and can motivate withdrawal from a damaging situation and protection of a damaged body part (Lynn, 1984). However, withdrawing from injurious behavior imposes costs if the behavior is potentially fitness enhancing. In such situations, organisms face a tradeoff between avoiding tissue damage and missing opportunities to increase fitness. The relative weights of the associated costs and benefits will vary between individuals and across contexts. Given stronger sexual selection and greater reproductive variance among men compared to women, men are generally expected to engage in costlier, more injurious behaviors in contexts that can augment mating success, such as contest competition. Ancestral men who disengaged from or avoided contests may have suffered fewer injuries but left fewer offspring. The experience of less pain for a given stimulus may represent a proximate mechanism shaped by sexual selection to facilitate continued engagement in contests despite injury. If so, then men would be expected to exhibit less pain sensitivity and greater pain tolerance, perhaps especially in competitive contexts.

These predictions have been borne out. Relative to women, men can undergo more intense stimulation such as physical pressure on the body for longer periods of time before experiencing pain, they are able to tolerate more pain, and these effect sizes are moderate to large (Fillingim et al., 2009; Riley et al., 1998). Moreover, in one study, men experienced analgesia after competition against a same-sex competitor regardless of exercise, whereas women experienced analgesia only after exercise (Sternberg et al., 2001).

Anatomical Adaptations for Male Contests

While observational studies of aggression among primates provide the most direct evidence of contest competition, another relevant line of evidence concerns body size sexual dimorphism. In a sample of 18 species of anthropoids representing 12 genera, Mitani et al. (1996) confirmed the relationship between body size dimorphism and OSR expected from sexual selection theory. In the human lineage, sexual size dimorphism exhibits great antiquity revealed through a large, albeit fragmentary, hominin fossil record dating back millions of years (Plavcan, 2012). Yet, research on levels of sexual dimorphism in earlier hominins is equivocal. For example, the best-represented fossil hominin, *Australopithecus afarensis*, which lived roughly 3–4 million years ago, has been alleged by some researchers (Gordon et al., 2008; Lockwood et al., 1996; McHenry, 1991), but not others (Reno and Lovejoy, 2015; Reno et al., 2010; Reno et al., 2003), to have exhibited a level of sexual dimorphism commensurate with that of extant gorillas and orangutans.

By the time of *Homo erectus*, whose existence covers most of the last 2 million years, sexual dimorphism had reached the approximate levels of modern *Homo sapiens* (Antón, 2003). Among modern humans, skeletal dimorphism is consistent with a primate species in which males are 45%–50% larger (Gordon et al., 2008). Compared to women, men possess 31%–43% more fat-free body mass (Lassek and Gaulin, 2009; Wells, 2012), 61% more muscle mass overall, and 75% more upper-body muscle mass (Abe et al., 2003; Lassek and Gaulin, 2009). As a result, the average man is stronger than 99.9% of women (Lassek and Gaulin, 2009).

Men with a masculine, muscular body shape have more sex partners (Frederick and Haselton, 2007; Hill et al., 2013; Lassek and Gaulin, 2009), particularly in short-term relationships (Rhodes et al., 2005), and begin having sex at an earlier age (Hughes and Gallup, 2003) than do less masculine men. Larger men, both in terms of height (Frederick and Jenkins, 2015; Mueller and Mazur, 2001) and body mass (Frederick and Jenkins, 2015), also report more sex partners. Although mating success does not necessarily translate into reproductive success among natural fertility populations, positive relationships have been observed between men's reproductive success and both height (Mueller and Mazur, 2001; Pawlowski et al., 2000) and physical prowess (Chagnon, 1988; Smith et al., 2003).

Men also appear designed to weather bodily insults, particularly to the head, which is disproportionately targeted (Shepherd et al., 1988) and injured (Carrier and Morgan, 2015) in fights. Brink et al. (1998) examined 2432 bodily injuries in 1156 men and 325 women in Denmark for a one-year period in the mid-1990s, reporting 69% to have been craniofacial, with injuries in both sexes tending to be produced by blunt force at close range. Indeed, sexual dimorphism in cranial robusticity may partly be attributable to physical violence among men, as features such as more robust mandibles and brow ridges may protect against catastrophic facial fractures (Carrier and Morgan, 2015; Puts, 2010). Women generally do not experience commensurate levels of physical aggression (Campbell, 2013; Daly and Wilson, 1988) and display less cranial robusticity and fewer cranial injuries (Carrier and Morgan, 2015; Shepherd et al., 1988).

Weapons Use

Contest competition often favors the evolution of anatomical weapons, such as antlers, horns, and, in primates, large canine teeth. Yet, compared with our closest living relatives, both men and women possess relatively small canines, and we lack substantial canine-size sexual dimorphism (Wood et al., 1991). Diminution in canine size and a departure from the CP_3 honing complex, a typical ape feature, begins with one of the earliest hominin candidates (7 to 6 Ma), *Sahelanthropus tchadensis* (Brunet et al., 2002), and continues through the Pliocene genera *Ardipithecus* (Suwa et al., 2009) and *Australopithecus* (White et al., 2000) to *Homo* after 2.5 Ma (Suwa et al., 2009).

One hypothesis for reduction in canines and other skeletal features related to biting is that canine weaponry was supplanted by handheld weapons and forelimbs freed by bipedal locomotion (Carrier, 2011; Darwin, 1871; McHenry, 1991). Clubs, spears, and hurled stones may have obviated biting by keeping enemies at a distance in the way that antlers appear to have replaced large maxillary canines in several deer species (Barrette, 1977). In addition, our shift to habitual bipedalism and its associated orthograde posture enhanced the injuriousness of physical blows (Carrier, 2011).

Male chimpanzees make and use tools, including using branches in dominance displays (but not as offensive weapons; van Lawick-Goodall, 1968), suggesting that tools have been used since the last common ancestor of *Pan* and *Homo*. While the earliest evidence of a weapon-inflicted wound has been dated to roughly 100,000 years ago (Pickering et al., 2000), the emergence of manufactured stone tools by at least 3.4 million years ago (Harmand et al., 2015; McPherron et al., 2010) suggests that handheld weapons were used far earlier. Indeed, it is difficult to imagine an ancestral species with the mental capacity to shape stones for use as cutting tools, and with males fighting over mates, in which males would not also utilize branches, bones, antlers, and other materials in their environment as weapons.

The use of projectile weapons such as hurled rocks and spears may have contributed to the very large male advantage in throwing velocity (3.5 standard deviations by age 12 years; Thomas and French, 1985), as well as men's 1.5 standard deviation advantage in targeting and avoiding projectiles (Watson and Kimura, 1991). This targeting difference remains large after controlling for experience (Watson and Kimura, 1991) and appears to depend developmentally on early androgen exposure (Hines et al., 2003). Across societies, the manufacture and use of weapons against same-sex rivals is ubiquitous among men and rare among women (Archer, 2004; Ellis et al., 2008; Smith and Smith, 1995; Warner et al., 2005).

The development of handheld weapons represented a watershed moment in hominin evolution, imbuing physical contests among men with a previously unknown degree of lethality. Moreover, for the first time in primate evolution, individuals were able to aggress from a distance, reducing the advantage of anatomical weaponry and possibly spurring the diminution of sexual dimorphism in body, and especially canine, size. This inference has important implications: if the use of handheld weapons is responsible for reduction in the typical trappings of primate intrasexual selection, then an examination of body size dimorphism and canine size dimorphism may lead us to underestimate the intensity of contest competition over the evolution of our species.

Dominance Displays

Traits such as physical aggression, pain tolerance, size, strength, facial robusticity, and weapons use may have served to make men more competitive in physical contests. However, physical violence is costly energetically and in terms of risk of injury or death, as well as risk of retribution (eg, Beckerman et al., 2009; Daly and Wilson, 1988). Across species, male contests frequently involve displays and mutual assessment of formidability, often ending when one rival submits before either is injured (see Smith and Parker, 1976 for a discussion of asymmetric contests). While the costs of submission in terms of reduced social status and mating opportunities may be high, the costs of defeat may be higher. As a result, ancestral men capable of accurately assessing rivals' physical formidability likely obtained a selective advantage (Sell et al., 2009, 2010; Wolff and Puts, 2010). Because male–male aggression is culturally ubiquitous (Daly and Wilson, 1988) and characterizes all extant apes (Puts, 2010), we can be confident that there was selective pressure for such acuity ancestrally.

Men are therefore expected to attend closely to the formidability and volatility of their same-sex competitors, to exercise caution accordingly, and to use nonviolent means such as threats and negotiation to obtain status and valued resources. Men appear to utilize cues such as facial appearance (Carrier and Morgan, 2015; Sell et al., 2014; Sell et al., 2009; Zilioli et al., 2014), muscularity (Hill et al., 2013), and height (Stulp et al., 2015) to assess one another's formidability. However, some traits that influence dominance perceptions may have been shaped by selection specifically to signal formidability, as we now discuss.

Behavioral Displays of Formidability

Men may avoid potentially deadly conflict by displaying their formidability to rivals in diverse ways, including greater risk-taking behavior when peers are present (Ginsburg and Miller, 1982; Morrongiello and Dawber, 2004) and when those peers are male (Ermer et al., 2008). In support of this, research has associated dangerous risk-taking with perceptions of physical formidability (Fessler et al., 2014), suggesting that risk-taking and acuity to risk-taking may have evolved for success in contests.

Among the Yanomamo, contests often involve "shouting matches, chest pounding duels, side slapping duels, club fights, fights with axes and machetes, and shooting with bows and arrows with the intent to kill" (Chagnon, 1988, p. 986). Among the Meriam of Australia, the hunting of large sea turtles is physically demanding, potentially injurious, and may function to signal formidability to other men (Bliege Bird et al., 2001; Smith et al., 2003). Optimal foraging and reciprocal altruism are unlikely to explain turtle hunting behavior. Turtle hunting is inefficient as a means of procuring food, hunters typically give away the meat at feasts, and this altruism tends not to be reciprocated. In addition, women do not report greater attraction to turtle hunters, so turtle hunting does not appear to function in mate attraction either (Smith et al., 2003). However, turtle hunting is respected by men, and turtle hunters report earlier onset of sexual behavior and larger numbers of sex partners than nonhunters, as well as 2.4 times greater lifetime reproductive success, with an even larger difference for hunt leaders (Smith et al., 2003).

Men's greater average interest in playing and observing sports, both in the contemporary United States (Deaner et al., 2012) and across traditional societies (Deaner and Smith, 2013), may also reflect selection for displays of formidability—as well as for physical aggression, interest in competition, and the predisposition to engage in activities that build strength and hone skills useful in contests. The male bias in sports participation is striking: in a sample of 50 societies taken from the Human Relations Area Files, males participated in 95% of all sports, females in only 20%, with men predominating especially in combat-related sports (Deaner and Smith, 2013).

Anatomical Threat Displays

Humans are among the most visually sexually dimorphic primates (Dixson et al., 2005), and recent research suggests that at least some conspicuous traits may function to increase men's appearance of formidability. For example, beards and eyebrow hair grow at puberty in males and may signal formidability through associations with physical maturity and testosterone levels and by increasing the apparent size of the jaw and brow (Guthrie, 1970;

Muscarella and Cunningham, 1996; Neave and Shields, 2008). Male faces with beards are rated as more dominant but not more attractive than the same faces clean-shaven (Dixson and Vasey, 2012; Muscarella and Cunningham, 1996; Neave and Shields, 2008).

Likewise, both correlational (Hodges-Simeon et al., 2010) and experimental (Feinberg et al., 2005; Puts et al., 2006, 2007; Wolff and Puts, 2010) research shows positive relationships between vocal masculinity, such as low pitch and vocal timbre, and perceptions of men's dominance. Men's vocal tracts are 15% longer, and their vocal folds 60% longer, than women's (Fant, 1960; Titze, 2000), several times the 7%–8% expected from the sex difference in stature (Gaulin and Boster, 1985). Elevated testosterone levels at puberty cause males' vocal folds to grow longer and thicker than those of females, both absolutely and relative to overall body growth (Harries et al., 1997; Hollien et al., 1994). Men's larger vocal folds consequently vibrate at a fundamental frequency approximately half that of females during phonation, which we perceive as a lower pitch. Similarly, males' larynges descend a full vertebra lower than females' at puberty (Fitch and Giedd, 1999), producing a longer vocal tract and resulting in lower, more closely spaced formant frequencies and a deeper, richer-sounding timbre.

In a cross-cultural sample of voice recordings, men accurately assessed physical strength from the voice even when listening to unfamiliar languages (Sell et al., 2010). Although pitch and timbre track body size within-sex only modestly (González, 2004; Lass and Brown, 1978; Pisanski et al., 2014; Rendall et al., 2005), masculine voices have also been associated with physical aggressiveness, testosterone levels, and peer evaluations of fighting ability (Hill et al., 2013; Puts et al., 2012a). It may be the case that masculine voices are reliable signals of dominance even while masculine voices are only modestly associated with any particular correlate of dominance.

Dominance, Mating, and Reproductive Success

Displays of formidability, whether behavioral or anatomical, may have contributed to mating success among ancestral men by increasing dominance (coerced social status) and prestige (freely conferred deference; Henrich and Gil-White, 2001). Displays of formidability may influence prestige because dominant men can make strong leaders and powerful allies and may also possess skills worthy of emulation. Indeed, experimental evidence suggests that social status is conferred upon dominant men in proportion to their being viewed as likely to generate benefits for the group via within-group enforcement and between-group representation (Lukaszewski et al., 2015). Both dominance and prestige can thus aid in social competition over all contested resources, including food and territory, as well as mates (West-Eberhard, 1983). Indeed, success in competition with other males has been shown to increase men's preferences for feminine female mates (Welling et al., 2013), suggesting that success in male–male competition increases access to desirable sex partners.

In non-Western samples, both dominance and prestige have been associated with increased mating and reproductive success in men (Chagnon, 1988; Smith et al., 2003; von Rueden et al., 2011). However, this does not imply that sexual selection has favored high levels of unrestrained male belligerence. As noted previously, physical aggression is costly and should be dependent upon context, including the likelihood of defeat and the threat of retribution. For example, among the extremely bellicose Waorani of Ecuador, men who participated in the most raids of other villages did not have more wives or offspring (Beckerman et al., 2009). Although failure to avenge homicides may be perceived as a sign of weakness among the Waorani, raiding also brought immediate retribution against the raider's village. It is thus possible that a moderate level of raiding represented the optimal balance between the costs of retribution and the costs of appearing weak.

Among Western undergraduate students, a component of mating success—number of sex partners in the past year—was positively related to self-rated fighting ability in two samples (Wolff and Puts, 2010), and male acquaintances' ratings of fighting ability, as well as size and muscularity, in another sample (Hill et al., 2013). Displays of physical competitive ability such as sports performance (Faurie et al., 2004; Honekopp et al., 2007) and gang membership (Palmer and Tilley, 1995) have also been positively related to mating success.

In addition, traits that influence perceptions of dominance predict mating and reproductive success. For example, a masculine, dominant-sounding voice has been associated with greater mating success in samples of US undergraduates (Hill et al., 2013; Hodges-Simeon et al., 2011; Puts, 2005), as well as with greater reproductive success in a sample of Tanzanian foragers (Apicella et al., 2007). Likewise, dominant facial appearance has been found to predict eventual military rank and reproductive success among military cadets (Mueller and Mazur, 1997).

Coalitional Aggression

Males are more likely than females to kill and be killed by conspecifics among our closest living relatives, chimpanzees (Wrangham et al., 2006), who, like humans, engage in coalitional aggression. Wrangham and Glowacki (2012, p. 20) argue that humans generally conform to the pattern seen in chimps: "consistent intergroup hostility, safe killing, and benefits from intergroup dominance." Thus, aggressive behavior among allied groups of males, which presents early via boyhood competition (Geary et al., 2003), has likely not only long been a feature of human life (eg, Bamforth, 1994; Frayer, 1997), but may also be a more primitive feature of our primate heritage. There are, however, important distinctions that set humans apart. Notably, hunter-gatherer groups display an ability for peacemaking involving protracted periods of nonviolence toward rival groups that is uncharacteristic of chimpanzees. As Wrangham (1999, p. 18) writes, "Peace is the normal human condition, in the sense that most human groups, for most of the time, are not at war."

A further difference is that chimpanzees engage in far more overt aggression overall, but human aggression is more often lethal, so that chimps and humans living in subsistence societies exhibit similar levels of lethal aggression (Wrangham et al., 2006). For example, the Arnhem Land people of Australia are characterized by an unusually high rate of physical aggression among human populations (Wrangham et al., 2006) but nevertheless display a rate of physical attack two orders of magnitude below that of chimpanzees. In light of this, a comparison with chimps seems apt only to a point in informing our understanding of the possible evolutionary history of human violence. Perhaps the lethality of human weapons elevates the importance of threats, deference, and peacemaking in relation to physical attacks when negotiating intragroup dominance hierarchies and intergroup conflict.

In addition, the substantial death tolls attributable to violence recorded among traditional human societies occur at a level of social complexity greater than physical contests between two males. Of importance is the presence of "organized and sanctioned group violence that involves armed conflict, including confrontations that combatants recognize may result in deliberate killing," as Webster (1998, pp. 313–314) has defined warfare. Conflicts, according to Webster, are perpetrated "with the intent of maintaining the status quo or bringing about a shift of power relations, usually the latter." This definition is similar to understandings of coalitional violence in chimpanzees, which Wrangham's (1999) imbalance-of-power hypothesis argues is contingent on (1) hostility and (2) power asymmetries among groups. The psychological traits that might be favored in the service of coalitional aggression include, as Wrangham (1999, p. 23) suggests, "a tendency to classify others as in-group or out-group, to regard members of out-groups as potential prey, to be alert to (or search for) power asymmetries between in-group and out-group parties, and to be ruthless in attacking out-group parties when the perceived power asymmetry is sufficiently great."

While there are no doubt myriad proximate motivations for organized group violence in our species, such as a desire for slaves, territory, political control, revenge, resolution of economic disagreements, and more fruitful environments (eg, Keeley, 1996), selection ultimately favors traits that contribute to reproduction. Hence, it is at least parsimonious to hypothesize that reproduction lies at the root of coalitional violence, as well. Even when a desire for resources or political control is the immediate cause, these desires may themselves have been forged in the fires of mating competition.

By way of raiding, men are able to forcibly procure female mates through "bride theft," which appears to be a species-typical behavioral trait (Ayres, 1974). Across 10 traditional Amazonian societies, women were captured during 26% of raids occurring within a language family and 54% of raids occurring across language families (Walker and Bailey, 2013). Intergroup aggression among both chimpanzees (Mitani et al., 2010) and humans (Bollig, 1990; Mathew and Boyd, 2014) may additionally enable males to obtain territory and resources that contribute to their mating success. Among human subsistence societies, men appear well aware of what is in the reproductive balance. As Chagnon (1988) reports of the Yanomamo, a desire for women is the main impetus for engaging in warfare, and, importantly, this is the top reason given by Yanomamo, a finding not unique to that particular society. While reasons for warfare and lesser forms of coalitional violence are undoubtedly complex, the desire for mates is acknowledged as a nearly ubiquitous motivation for preindustrial warfare, even among scholars generally unsympathetic to sociobiological theories of behavioral evolution (eg, Keeley, 1996).

Male coalitional violence, regardless of its most immediate cause, has produced an archaeological record riddled with evidence of violent, often lethal, physical aggression among men stretching back beyond the advent of agriculture (Lahr et al., 2016). In one North American paleoindian burial site, roughly 16% of skeletal remains indicate violent death, 5% showing evidence of having been scalped, and 4% decapitated (Milner et al., 1991). Moreover, males account for a higher percentage of victims of violence among all individuals of known sex. This is far from an aberrant finding, with other burial sites yielding similar results. Andrushko et al. (2005) estimated from a burial site of 59 males and 86 females that at least 20% of males, but only 2% of females, experienced a violent death, likely the result of warfare, as evinced by perimortem amputation. The men, furthermore, tended to be young adults, which is the age range of fiercest competition for mates.

Of course, the relationship between male coalitional violence and reproductive success is not always linear and positive. As noted earlier, among the Waorani of Ecuador, Beckerman et al. (2009) report poorer reproductive success as well as exceptionally high mortality rates among the most ardent warriors. Among humans everywhere, there are great costs associated with aggression (Chagnon, 1988). This may result in a curvilinear relationship between aggression and reproductive success, with a maximum that is likely contingent on numerous aspects of the social environment. There would have thus been great benefit ancestrally associated with correctly assessing the potential costs and likelihood of success in a raid, just as there would have been great benefit in correctly assessing the physical formidability of a single male rival. Just as there would be costs to stealing another man's mate, there are costs to participating in a raid to steal the mates of many men. The costs and benefits associated with intragroup aggression may have selected for high levels of intragroup cooperation specifically in the context of warfare. Indeed, experimental research has shown males to exhibit greater group-level contribution in the face of competition from other groups (Van Vugt et al., 2007).

ALTERNATIVES TO MALE CONTESTS

We have reviewed evidence that men's phenotypes are partly products of ancestral contest competition for mates. Men exhibit each of the traits typical of species with male contests, and these traits appear to have been shaped by sexual selection; they are sexually dimorphic and predict men's mating success as well as success in contest competition. Many of these traits (eg, deep voices, beards, muscularity) also emerge at sexual maturity. The exceptions are behaviors that require years of practice to hone relevant skills: fighting, weapons use, behavioral displays of formidability, and coalition formation (eg, Pellis and Pellis, 2007; Thomas and French, 1985)—all of which exhibit prepubertal sex differences, although the sexes may further diverge at puberty. However, we have not yet considered alternative hypotheses: whether some of the previously mentioned traits were shaped by other selective pressures, or arose as byproducts of selection on developmentally correlated traits.

For example, some human sexual dimorphisms may partly be products of a sexual division of labor that is essentially ubiquitous across forager societies: men spend more time hunting, especially larger game, and women spend more time gathering or hunting smaller game (Murdock, 1967). Thus, ecological selection may have contributed to men's greater size, strength, and weapons proficiency to the extent that these contributed to hunting success ancestrally (Kaplan et al., 2000). However, other of men's traits, such as beards, deep voices, more robust faces, and high levels of same-sex aggression, are not easily understood as adaptations for hunting. In addition, given that male contests and sexual size dimorphism probably characterized the common ancestor of the great apes, contest competition likely predates specialized hunting and the human sexual division of labor by several million years. Hence, it is more likely that the sexual division of labor is partly a consequence rather than the initial cause of these anatomical dimorphisms, although hunting likely imposed additional selection pressures on these male traits.

Some aspects of men's phenotypes may also have been produced via female choice, or through a combination of contests and female choice. Because traits that evolve in contest competition are often costly to produce and maintain and are constantly tested by competitors, such traits may represent honest indicators of heritable fitness, and females may consequently evolve preferences for them (Berglund et al., 1996). On the one hand, masculine bodies, faces, and voices in men have indeed been found to increase attractiveness to women (Frederick and Haselton, 2007; Puts et al., 2012b). On the other hand, the influence of facial and vocal masculinity on ratings of dominance is considerably larger and more consistently positive than the effects on attractiveness (Puts et al., 2012b). Recent work suggests that male facial masculinity may not be universally preferred by women across human societies, whereas it much more consistently conveys the impression of aggressiveness (Scott et al., 2014). Likewise, beards reliably increase perceptions of age, aggression, dominance, and social status across societies, but generally decrease attractiveness to women (Dixson and Vasey, 2012; Muscarella and Cunningham, 1996; Neave and Shields, 2008). Furthermore, in samples spanning Western (Hill et al., 2013), traditional agricultural (Llaurens et al., 2009), and preindustrial (Smith et al., 2003) societies, men's mating success has been found to relate more strongly to dominance among men and the traits that contribute to dominance than to attractiveness to women. Across the suite of male secondary sexual characteristics, then, selection for success in physical contests may have been either attenuated or augmented by selection for attractiveness to females. In general, however, men's traits function far more effectively in the context of male contests than in mate attraction, and thus they do not appear to have evolved primarily as sexual ornaments to attract women.

Another possibility is that some of men's traits represent developmental byproducts of male body size or testosterone levels. Strength increases with body mass and height (Balogun et al., 1991), for example, although other male traits are not known to relate to body size (eg, beards) or relate only weakly (eg, voice pitch; Pisanski et al., 2014). However, even traits that are correlated with size are far more sexually dimorphic than would be predicted from sex differences in size alone (Puts et al., 2012b). Similarly, androgens such as testosterone play important roles in the development of male-typical traits, so one might conjecture that these traits are merely developmental side-effects of androgens. This viewpoint confuses proximate and ultimate explanation, leaving unresolved the question of why humans have evolved to respond to testosterone by growing facial hair and longer-thicker vocal folds, for example. Why instead do we not respond to testosterone by growing antlers, as in red deer (Suttie et al., 1995), or canines, as in many other primates (Van Wagenen and Hurme, 1950)? Why does testosterone not increase paternal investment, as in the California mouse (*Peromyscus californicus*) (Gleason and Marler, 2013), rather than having the opposite effect, as it does in many vertebrates, apparently including humans (Kuzawa et al., 2009; Puts et al., 2015b)? Clearly, different species, even closely related ones, can evolve quite different responses to the same hormones. An evolutionary history of male contests parsimoniously explains why, in humans, a particular constellation of sexually dimorphic traits including large size may be developmentally linked to testosterone and to each other.

A final alternative to contest competition in our hominin ancestors is phylogenetic inertia—the idea that we have inherited our traits from ancestral species rather than experiencing selection for these traits in our own species. Fossil and comparative evidence indicate that we did indeed inherit traits such as greater male size and aggression from an ancient hominin ancestor. However, for other traits such as deep voices (Puts et al., 2016), beards, and the use of handheld weapons, this appears not to have been the case. Even for traits such as greater male size and aggression that were likely sexually dimorphic in our common ancestor with chimpanzees, we would expect considerable reduction in modern humans if these traits were not functional over recent hominin evolution, given their substantial costs. And yet, as discussed earlier, men's physical aggression is equally lethal to that of male chimpanzees, and we are more sexually dimorphic than chimpanzees in both skeletal size and fat-free mass.

Despite the comparatively strong overall evidence for the importance of contest competition over men's evolution, each of these alternative factors may have played a role. These are not mutually exclusive alternatives; any aspect of the phenotype can experience multiple selection pressures, as well as responding to selection on other traits with which it is developmentally correlated.

CONCLUSION

We have reviewed multiple converging lines of evidence supporting a role for contest competition in shaping the human male phenotype. Sex differences in parental investment, reproductive rates, and reproductive variance; the OSR; and patterns of mating and marriage—all indicate a history of moderately strong sexual selection among our male ancestors.

Contest competition in particular tends to favor size, strength, aggression, weapons, and threat displays, and men display all of these features. Traits that point to an evolutionary past in which our male ancestors competed for mates through force and threat include a proclivity for same-sex violence including coalitional aggression, higher pain threshold and tolerance compared to women, increased body size and strength, facial robusticity, fashioning and use of weapons, beards, deep voices, and behavioral displays of formidability. This evidence is taken from research across fields ranging from human anatomy and physiology to psychology, ethnography, paleoanthropology, animal behavior, and archaeology. The alternative hypotheses that men's traits were shaped by selection for hunting ability, female mate choice, or selection operating on developmentally correlated traits—or that men's traits are consequences of phylogenetic inertia—can help account for some of the above aspects of men's phenotypes, but not others. The success of any hypothesis is contingent on a parsimonious explanation of the totality of evidence, and only contest competition accomplishes this. In some ways, we may be more gorilla-like, or chimp-like, than we prefer to suppose.

It is important to bear in mind, however, that while human nature includes a propensity for violence in both individual and coalitional forms, we are also capable of negotiation, compromise, and restraint. For a species currently numbering in the billions that now possesses weapons capable of bringing about its own annihilation, the importance of understanding our capacity for violence is more than academic—it can potentially illuminate and suggest solutions to problems of pressing societal concern.

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